Patterns of Polypore Distribution in the Lesser Sunda Islands, Indonesia. Is Wallace's Line Significant? 6

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Introduction

Indonesia has often played an important role in biogeographical research owing to its key position at the meeting point of the Asian and the Australian tectonic plates (Audley-Charles, 1987). Based on distributional patterns of mammals, birds and butterflies, Wallace (1860) drew a line across the Indonesian archipelago to mark the borderline between the Asian and the Australian biotas. Today, the biological significance of Wallace's line is considered outdated for many groups of organisms (Simpson, 1977; van Steenis, 1979; Touw, 1992; Hisheh *et al.*, 1998). However, some organisms have a distribution limited either to the Asian or to the Australian side of Wallace's line, as in the case for most genera of conifers and taxads (Schuster, 1972).

The Lesser Sunda Islands consist of two geologically distinct archipelagos. The northern archipelago, including Bali, Lombok, Sumbawa, Flores and Wetar, is volcanic in origin. It was formed during the Pliocene after the collision between the Australian and the Asian plate, about 15×10^6 years ago, Wallace's line lying between Bali and Lombok (Fig. 6.1). The islands of the southern archipelago, including Sumba, Timor and Babar, are non-volcanic and appear to belong to the Australian plate (Audley-Charles, 1987; Veevers, 1991). Little mycological research has been done in the Lesser Sunda Islands and no publications documenting their polypore mycota were found during this study, but Pirozynski (1983) and Sims *et al.* (1997) have discussed several distributional patterns of Australasian fungi.

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This chapter addresses the significance of Wallace's line for polypore distribution in some of the Lesser Sunda Islands from the northern archipelago, namely Bali, Lombok and Sumbawa. These islands were chosen for this study because of the position of the Wallace line coinciding as it does with the geological boundary between the Asian and Australian plates (Musser, 1981). When these plates approached each other, two biotas of independent origin were physically mixed.

In addition, the proximity of these islands to Bali Botanical Garden made logistics easier and Bali, Lombok and Sumbawa lie aligned to the east with Sumatra and Java, which have a relatively well known mycota of polypores (Suhirman and Núñez, 1995, 1996).

Similarities in polypore species composition between the different collecting localities were quantified. Using literature records, this analysis was extended to include Sumatra, Java, Papua New Guinea (PNG) and Australia in an attempt to explain polypore distribution patterns in Australasia according to Croizat's (1958) model of generalized tracks.

Polypore species lists were compiled for Sumatra, Java, Bali, Lombok, Sumbawa, PNG and Australia. These lists are based on published records (Imazeki, 1952; Cunningham, 1965; Steyaert, 1972; Ryvarden, 1981; Quanten, 1993; Suhirman and Núñez, 1995, 1996, 1998), and the authors' collections from Java, Bali, Lombok and Sumbawa at the beginning of the rainy season during 1994 and 1996. The type of forest in each collecting locality was specified (Table 6.1).

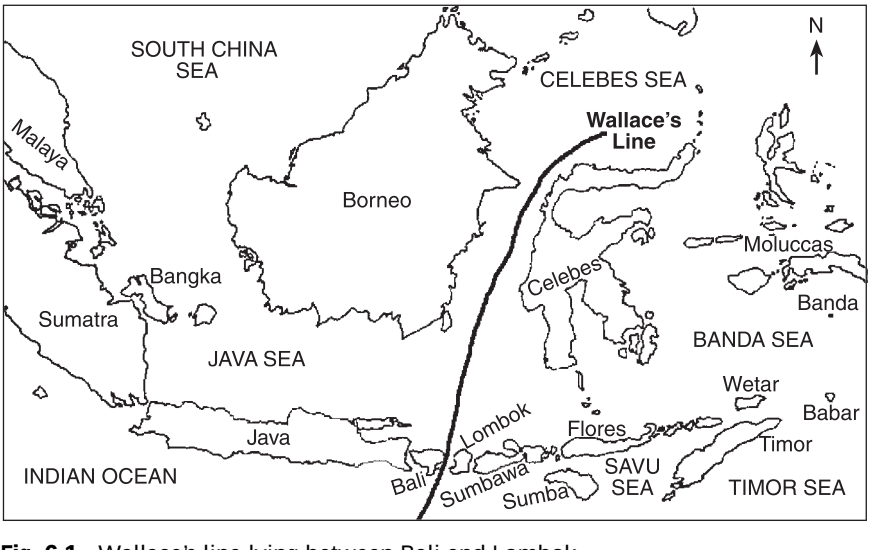

Fig. 6.1. Wallace's line lying between Bali and Lombok.

Table 6.1. Collecting localities in the Lesser Sunda Islands.

Bali monsoon Bali: Teluk Terima, Bali-Barat National Park, Jembrana province, 0–250 m a.s.l., 20–21 May 1994. Monsoon forest.
Bali lowland Bali: Gunnung Klatakan, Bali-Barat National Park, Jembrana province, 500–690 m a.s.l., 22–23 May 1994. Lowland rainforest.
Bali cloud Bali: Bukit Tapak, 1300–1700 m a.s.l., 25–26 May 1994. Cloud forest with *Casuarina junghuhniana* and *Podocarpus* sp.
Lombok lowland Lombok: Torean, Rinjani Mountain, 700–900 m a.s.l., 28–29 May 1994. Lowland rainforest.
Lombok cloud Lombok: Ponsuk forest, Sembalun, 1500–1600 m a.s.l., 1 June 1994 and 19–20 October 1996. Cloud forest.
Sumbawa monsoon Sumbawa: Kawinda, Tambora Mt, 450–860 m a.s.l., 25 October 1996. Monsoon forest.
Sumbawa cloud Sumbawa: Semonkat Brombosang, 1200 m a.s.l., 23–24 October 1996. Cloud forest.

The similarity index $S = 2c/(a + b)$ was used to quantify similarities in species composition between the different localities. In this formula, a and b are the number of taxa in locality a and b respectively, and c is the number of shared taxa between the two localities. The value of the index varies between 0 (no shared taxa) and 1.0 (identical species composition in locality a and b).

Results

A total of 102 species were identified from 626 collections sampled in Bali, Lombok and Sumbawa as listed in Table 6.2. However, 15 collections of 6 or 7 species remain unidentified resulting from either nomenclatural or taxonomic problems. In Java, Sumatra, Australia, PNG and the Lesser Sunda Islands the total was 375. *Ceriporia ferruginicincta* (Murrill) Ryv., and *Skeletocutis diluta* (Rajchenb.) A. David & Rajchenb. are new records for Asia.

The world distribution of the species collected in Bali, Lombok and Sumbawa is shown in Table 6.3. Most of the species were either pantropical (52%) or palaeotropical (25%). Australian species have not yet been recorded from the area, and only two Australasian species were collected, *Elmerina cladophora* (Berk.) Bres. and *Oxyporus cervino-gilvus* (Junghuhn) Ryv., both of which were found in the cloud forests of Lombok and Sumbawa. Two holarctic species were found: *Antrodiella semisupina* (Berk. & M.A. Curtis) Ryv. in Lombok cloud forest, and *Oxyporus populinus* (Fr.) Donk in Sumbawa cloud forest.

Table 6.2. Polypore species collected in Bali, Lombok and Sumbawa forest types.

Species	Bali monsoon	Bali lowland	Bali cloud	Lombok lowland	Lombok cloud	Sumbawa monsoon	Sumbawa cloud
Antrodiella liebmannii		*	*	*	*		
A. semisupina					*		
Bjerkandera adusta				*	*	*	
Ceriporia ferruginicincta						*	
C. mellea						*	
C. xylostromatoides							*
Cerrena meyenii						*	
Chaetoporellus latitans					*		*
Coriolopsis asper	*		*	*		*	
C. brunneo-leuca						*	
C. byrsina						*	*
C. caperata	*						
C. floccosa	*	*		*		*	*
C. glabrorigens							
C. sanguinaria		*					
C. telfarii	*						
Cyclomyces fuscus		*	*				
C. setiporus		*	*	*	*		
C. tabacinus			*	*	*		
Dictyopanus pusillus			*		*		
Earliella scabrosa	*	*	*		*		*
Echinochaete brachyporus		*					*
E. ruficeps	*						
Echinoporia hydnophora					*		
Elmerina cladophora					*	*	
Flavodon flavus	*	*		*	*	*	*

Fomitopsis carnea		*		*			
F. feei						*	*
F. rhodophaea	*	*	*				
G. applanatum			*		*		
G. australe	*						*
G. colossum	*	*					
G. lucidum			*		*		*
G. mastoporum			*				
Gloeoporus chroceopallens					*		
G. dichrous					*		*
G. thelephoroides	*	*			*	*	*
Hapalopilus albocitrinus					*		
Hexagonia hydnoides	*				*		
H. tenuis	*	*	*	*	*		*
Junghuhnia nitida		*	*				
Laetiporus sulphureus							*
Lenzites acuta							*
L. elegans							*
Loweporus inflexibilis					*	*	
L. roseoalbus		*			*		
Megasporoporia cavernulosa	*	*					
M. setulosa	*	*					
Microporellus obovatus				*	*		
Microporus affinis			*	*	*		
M. microloma			*			*	*
M. vernicipes	*	*	*	*	*		*
M. xanthopus	*	*	*	*	*	*	*

Continued

Table 6.2. (*Continued*).

Species	Bali monsoon	Bali lowland	Bali cloud	Lombok lowland	Lombok cloud	Sumbawa monsoon	Sumbawa cloud
Nigrofomes melanoporus	*	*	*	*	*		*
Nigroporus vinosus				*	*		
Oligoporus subcaesius		*	*	*	*		
Oxyporus cervinogilvus						*	*
O. populinus						*	
Perenniporia contraria							*
P. medulla-panis			*				
P. ochroleuca				*			
P. tephropora		*	*				*
Phellinus allardii						*	*
P. callimorphus							*
P. discipes						*	
P. fastuosus						*	*
P. gilvus	*						
P. glaucescens						*	*
P. lamaensis			*		*		*
P. noxius							*
P. pachyphloeus							*
Phylloporia chrysita	*	*		*			
P. spathulata				*			
Polyporus arcularius					*	*	*
P. dictyopus		*	*		*		
P. grammocephalus		*	*	*			*
P. tenuiculus	*	*	*	*	*		
P. udus							*
Protomerulius caryae					*		

Pseudofavolus cucullatus	*						
P. miquelii	*	*					
Pycnoporus sanguineus	*	*					*
Rigidoporus dextrinoideus					*		
R. lineatus			*		*		
R. microporus			*	*			
R. vinctus		*	*		*		*
Schizophyllum commune					*		
Schizopora flavipora		*	*	*			*
S. paradoxa		*	*			*	
Skeletocutis diluta			*	*	*	*	*
S. lenis							*
S. nivea					*	*	*
Theleporus calcicolor					*		*
Tinctoporellus epimiltinus		*	*	*	*		*
Trametes cingulata		*	*			*	
T. lactinea	*						
T. menziezii		*					*
T. mimetes		*					
T. socotrana					*		
T. versicolor			*		*		
Trichaptum durum		*	*	*	*	*	*
Wrightoporia tropicalis							*

Table 6.3. World distribution of polypores collected in the Lesser Sunda Islands. The highest and lowest scores are shown in bold.

	Number	Percentage
Cosmopolitan	18	17.5
Pantropical	**52**	**51**
Palaeotropical	25	24.5
Australasian	2	2
Asian	3	3
Australian	**0**	**0**
Holarctic	2	2
Total	102	

The total number of species collected in each locality and the unique component, that is, the subset of species found in each locality and nowhere else, are shown in Table 6.4. Total numbers ranged from 45 species sampled in Sumbawa cloud forest to 23 species in Bali monsoon forest. Only three species were common to all localities: *Hexagonia hydnoides* (Schwartz) M. Fidalgo, *Microporus vernicipes* (Berk.) Kuntze and *Microporus xanthopus* (Fr.) Kuntze.

Similarity Indices

The similarity indices and numbers of species shared between the sampled localities are shown in Table 6.5. The highest similarity index (0.59) and highest number of shared species (24) were found between the cloud forests of Bali and Lombok. The lowest similarity index (0.19) was found between the lowland forest of Lombok and the monsoon forest of Sumbawa.

Similarity indices for the three Lesser Sunda Islands and Java + Sumatra, a combination representative of the Asian plate, have been compared, and also with Australia + PNG, a combination representative of the Australian plate (Table 6.6). In Table 6.6, the three Lesser Sunda Islands are first shown as a single local-

Table 6.4. Total species numbers and unique components (i.e. species found in one locality and nowhere else) for each locality studied in the Lesser Sunda Islands. The highest and lowest species numbers are shown in bold.

	Total	Unique component
Bali monsoon	**23**	4
Bali lowland	39	6
Bali cloud	36	**3**
Lombok lowland	25	**3**
Lombok cloud	44	9
Sumbawa monsoon	28	8
Sumbawa cloud	**45**	**10**

Table 6.5. Similarity indices between the different collecting localities. The highest and lowest scores are shown in bold. The number of shared species is indicated in parentheses.

	Bali lowland	Bali cloud	Lombok lowland	Lombok cloud	Sumbawa monsoon	Sumbawa cloud
Bali monsoon	0.55(17)	0.27(8)	0.33(8)	0.24(8)	0.24(6)	0.35(12)
Bali lowland		0.58(15)	0.47(15)	0.41(17)	0.23(8)	0.45(19)
Bali cloud			0.52(16)	**0.59(24)**	0.22(7)	0.32(16)
Lombok lowland				0.49(17)	**0.19(5)**	0.28(10)
Lombok cloud					0.22(8)	0.45(20)
Sumbawa monsoon						0.41(15)

ity, then they have been divided according to their placement on the Asian (Bali) or the Australian (Lombok + Sumbawa) tectonic plates. As a single locality, the Lesser Sunda Islands have higher similarity indices when compared with Java + Sumatra (0.53) than when compared with Australia + PNG (0.40). However, the highest similarity index was obtained between Bali and Lombok + Sumbawa (0.55, Table 6.6).

Discussion

Species composition in Bali, Lombok and Sumbawa

The results of these surveys should be regarded as preliminary, as much collecting remains to be done in the area. This is particularly applicable to the non-volcanic islands of the southern archipelago of the Lesser Sunda Islands, including Sumba, Timor and Babar.

No sharp demarcation line for polypore distribution can be drawn between Bali, on the Asian plate, and Lombok + Sumbawa, on the Australian plate, which accords with previous work on angiosperms (van Steenis, 1979) and mosses (Touw, 1992). As a general pattern, species numbers were highest in

Table 6.6. Similarity indices in the Pacific Australasian region. The Lesser Sunda Islands are treated as a single locality (LSI), or as two localities on either the Asian or the Australian plate (i.e. Bali or Lombok or Sumbawa). PNG, Papua New Guinea. The highest value is shown in bold, and the number of shared species in parentheses.

	LSI	Bali	Lombok + Sumbawa	Australia + PNG
Java+Sumatra	0.53(69)	0.43(47)	0.46(56)	0.51(116)
Bali			**0.55(40)**	0.30(54)
Lombok + Sumbawa				0.33(64)
LSI				0.40(81)

the cloud forests and lowest in the monsoon forests. The low species numbers in the monsoon forests were probably largely attributable to collecting having been at the end of the dry season both in 1994 and in 1996.

Species unique to each locality were highlighted in an attempt to identify any endemic elements in the area. However, these unique components were always of either Asian or palaeotropical character and therefore the majority are likely to be found in other localities in the area when more collecting is undertaken, especially during the rainy season.

Similarity indices

The similarity indices obtained from Bali, Lombok and Sumbawa do not indicate any clear difference between the polypore mycota on either side of Wallace's line. The highest similarity index was obtained between Bali and Lombok cloud forests, on opposite sides of Wallace's line (Table 6.5). The polypore mycota of Bali, Lombok and Sumbawa was more similar to that of Java + Sumatra (Asian plate) than to that of Australia + PNG (Australian plate), regardless of whether the three Lesser Sunda Islands were considered as a single locality or as two localities separated by Wallace's line (Table 6.6).

Quanten (1993) found that there were twice as many Asian polypore species in PNG than Australian ones, even if PNG lies to the east of Wallace's line. She attributed this fact to the distribution of the higher plant vegetation types: 'the Indo-Malayan region is dominated by rainforest, while only a small area of Australia is covered by this vegetation type'.

In general, the highest similarity indices were obtained when comparing either lowland rainforest with cloud forest localities, or two cloud forest localities (Table 6.5). This indicates that the forest type is a more important factor for species composition than the islands' geographic position relative to Wallace's line.

Van Steenis (1984) established a floristic zonation in Malesia according to altitude. He defined a tropical zone (0–1000 m), a submontane zone (1000–1500 m), and a montane zone (1500–2400 m). Our study shows that polypore distribution does not follow the same zonation as angiosperms, since localities showing highest similarity indices ranged from 500 to 1700 m altitude (Tables 6.1 and 6.5).

Sumbawa monsoon forest had the lowest similarity indices when compared with other localities, a preliminary result which, due to limited collecting, should be treated with caution.

Species distribution in Pacific Australasia

The species lists compiled for the Pacific Australasian regions of Java, Sumatra, Australia and PNG showed that both Asia and Australia can be characterized

by groups of species that do not cross Wallace's line. Asian examples include *Daedalea incana* (Lév.) Ryv., *Haddowia aetii* Steyaert, *Humphreya endertii* Steyaert, *Hymenogramme javanensis* Mont. & Berk. and *Polyporus pervadens* Corner, whereas examples from Australia include *Australoporus tasmanicus* (Berk.) P.K. Buchanan & Ryv., *Dichomitus epitephrus* (Berk.) Ryv., *Dichomitus leucoplacus* (Berk.) Ryv., *Laccocephalus sclerotinus* (Rodway) Núñez & Ryvarden and *Piptoporus australiensis* (Wakef.) G. Cunn. Other species, for example *Diacanthodes novoguienensis* (Henn.) O. Fidalgo and *Macrohyporia dictyopora* (Cooke) I. Johans. & Ryvarden, appear to have a Gondwanaland origin, as they occur in both Australia and South America. Hjortstam and Ryvarden (1985) and Rajchenberg (1989) have discussed the Gondwanaland element in South America and Australia.

In contrast, the Pacific Australasian lists also show that several species do cross Wallace's line. However, due to the lack of fossil polypores, the time and direction of migration have to be inferred from other indirect methods. Croizat (1958) established the 'generalized track' theory to explain species distribution in an area. According to this theory, the most probable distribution patterns are those shared by several organism groups and concord with the known geological history of an area. Several distribution patterns have been suggested for Pacific Australasia (Touw, 1992; Michaux, 1994) and several polypore species can be tentatively assigned to them as follows:

1. *Temperate Australasian species*. Parts of the present continental Asia, e.g. Myanmar, western Thailand, Malay Peninsula and Sumatra, were in Gondwanaland and drifted towards Laurasia during the Jurassic (Audley-Charles, 1987). Burbidge (1960) stated that several Australian temperate plants apparently migrated with the land. A similar event may have happened with several temperate Australian polypores, for example *Coltriciella tasmanica* (Cleland & Rodway) D.A. Reid, *Heterobasidion insulare* (Murrill) Ryv., *Inonotus setulosocroceus* (Cleland & Rodway) P.K. Buchanan & Ryv. and *Laccocephalum hartmanni* (Cooke) Núñez & Ryv., which are known from the Asian temperate mycota in Japan, China and far eastern Russia. However, none of these species was found in the Lesser Sunda Islands. It is important to note that none of these Australian polypore species is known from southern South America, therefore they may have evolved after the Australian–Antarctic plate separated from the rest of Gondwanaland in the middle Eocene, some 45 million years ago (Schuster, 1972).

2. *Disjunct species within continental Asia*. During the Pliocene glaciation maxima, species at higher latitudes in continental Asia, mostly from warm-temperate areas, migrated southwards. The sea level had decreased about 200 m and the montane vegetation limit had also lowered (Audley-Charles, 1987). As more humid conditions returned to the islands after the glaciations, the rainforests gained terrain in the lowlands. Several of the warm-temperate species were isolated in the mountains and are now scattered over Wallace's line in the cloud and wet forests of Lombok and Sumbawa; for example *Coriolopsis glabrorigens*

(C.G.Lloyd) T. Hatt., *Echinoporia hydnophora* (Berk. & Broome) Ryv., *Gloeoporus croceopallens* Bres. and *Hapalopilus albocitrinus* (Petch) Ryv.. As is the case for mosses showing the same distribution pattern (Touw, 1992), the above species are adapted to drought, and appear to require a dry period to complete their life cycle.
3. *Species crossing Wallace's line in both directions as the Australian continent approached Asia from the mid-Miocene* (Raven and Axelrod, 1972). Examples among the polypores include *Ceriporia ferruginicincta*, *Cerrena meyenii* (Klotzsch) L. Hansen, *Echinochaete ruficeps* (Berk. & Broome) Ryv., *Elmerina cladophora*, *Mollicarpus cognatus* (Berk.) Ginns, *Oxyporus cervinogilvus* and *Phellinus glaucescens* (Petch) Ryv.. Intensive and extensive collecting in the Lesser Sunda Islands, especially in those of the southern archipelago, is critical to determine the direction of migration. Most of the species mentioned above are of tropical character. In other organism groups, migration of tropical species appears to be mainly from the Asian rainforests to those of East Australia (Michaux, 1994). Of the species mentioned above, only *M. cognatus* has not been found in the Lesser Sunda Islands.

Conclusions

The polypore mycota in several Lesser Sunda Islands, southern Indonesia, on both sides of Wallace's line, Bali on the Asian plate, and Lombok and Sumbawa on the Australian plate, have been compared. The results are extrapolated to include known distribution patterns of polypores in temperate and tropical East Asia and Australia.

Most of the collected species in Bali, Lombok and Sumbawa (77%) were either pantropical or palaeotropical. The polypore mycota did not differ significantly on either side of Wallace's line. The type of forest ecosystem seems to be a more important factor in distribution patterns of polypores than the geographical situation with respect to Wallace's line.

On a wider geographical scale, several species were tentatively assigned to the following distribution tracks in Australasia:

1. Australian temperate species that were rifted to East Asia during the Cretaceous: *C. tasmanica*, *H. insulare*, *I. setulosocroceus*, *L. hartmanni*, these species were not found in the Lesser Sunda Islands.
2. Vicariant species with continental Asia after the Pliocene glaciation maxima, present today as a discrete group in the cloud forests of Lombok and Sumbawa: *C. glabrorigens*, *E. hydnophora*, *G. croceopallens*, *H. albocitrinus*.
3. Species transgressing Wallace's line in both directions as the Australian continent approached Asia from the mid-Miocene: *C. ferruginicincta*, *C. meyenii*, *E. ruficeps*, *M. cognatus*, *O. cervinogilvus*, *P. glaucescens*.

C. ferruginicincta and *S. diluta* are new records for Asia.

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